Social learning of arbitrary food preferences in bonobos

Gladez Shorland[a,*], Emilie Genty[a,b], Jean-Pascal Guéry[c], Klaus Zuberbühler[a,c]

[a] Department of Comparative Cognition, Institute of Biology, University of Neuchâtel, Rue Emile-Argand 11, 2000 Neuchâtel, Switzerland.

[b] Institute of Work and Organizational Psychology, University of Neuchâtel, Rue Emile-Argand 11, 2000 Neuchâtel, Switzerland.

[c] La Vallée des Singes Primate park, Le Gureau, 86700 Romagne, France.

[d] School of Psychology and Neurosciences, University of St Andrews, St Mary's Quad, South Street, St Andrews, KY16 9JP, Scotland, UK.

E-mail: E. Genty, emilie.genty@unine.ch; J-P. Guéry, jp.guery@la-vallee-des-singes.fr; K. Zuberbühler, klaus.zuberbuehler@unine.ch.

Corresponding author:
G. Shorland
gladez.shorland@outlook.com
Department of Comparative Cognition, Institute of Biology, University of Neuchâtel, Rue Emile-Argand 11, 2000 Neuchâtel, Switzerland.

* Correspondence: G. Shorland, Department of Comparative Cognition, Institute of Biology, University of Neuchâtel, Rue Emile-Argand 11, 2000 Neuchâtel, Switzerland.
e-mail address: gladez.shorland@outlook.com

Highlights

- Bonobos socially learn and copy the arbitrary food preferences of others.
- Bonobos copied others' arbitrary preferences of novel foods on first attempts.
- Subject age and exposure time have a positive effect on successful social learning.
- Copied food preferences can remain stable despite having better knowledge.

ABSTRACT

A fruitful approach to investigate social learning in animals is based on paradigms involving the manipulation of artefacts. However, tool use and elaborate object manipulations are rare in natural conditions, suggesting that social learning evolved in other contexts where fitness consequences are higher, such as discriminating palatable from noxious foods, recognising predators or understanding social hierarchies. We focussed on one such context by investigating whether bonobos socially learned others' arbitrary food preferences through mere observation. To this end, we trained two demonstrators to prefer or avoid distinctly coloured food items, treated with either a sweet or bitter agent. Demonstrators then displayed their newly acquired preferences in front of naïve subjects. In subsequent choice tests, subjects generally matched their choices to the demonstrators' preferred food colours, despite having already tasted the equally palatable colour alternative. Both age and exposure to demonstrator preference had a significant positive effect on the proportion of matched choices. Moreover, in a context where errors can be costly, social learning was instant insofar as six of seven subjects used socially learned information to influence their very first food choice. We discuss these findings in light of the current debate on the evolution of social learning in animals.

Social learning of arbitrary food preferences in bonobos

Gladez Shorland[a*], Emilie Genty[a,b], Jean-Pascal Guéry[c], Klaus Zuberbühler[a,d]

[a] Department of Comparative Cognition, Institute of Biology, University of Neuchâtel, Rue Emile-Argand 11, 2000 Neuchâtel, Switzerland.
[b] Institute of Work and Organizational Psychology, University of Neuchâtel, Rue Emile-Argand 11, 2000 Neuchâtel, Switzerland.
[c] La Vallée des Singes Primate park, Le Gureau, 86700, Romagne, France.
[d] School of Psychology and Neurosciences, University of St Andrews, St Mary's Quad, South Street, St Andrews, KY16 9JP, UK.

E-mail: E. Genty, emilie.genty@unine.ch ; J-P. Guéry, jp.guery@la-vallee-des-singes.fr; K. Zuberbühler, klaus.zuberbuehler@unine.ch

* Corresponding author:
G. Shorland
e-mail: gladez.shorland@outlook.com
Address: Department of Comparative Cognition, Institute of Biology, University of Neuchâtel, Rue Emile-Argand 11, 2000 Neuchâtel, Switzerland.

ABSTRACT

A fruitful approach to investigate social learning in animals is based on paradigms involving the manipulation of artefacts. However, tool use and elaborate object manipulations are rare in natural conditions, suggesting that social learning evolved in other contexts where fitness consequences are higher, such as discriminating palatable from noxious foods, recognising predators or understanding social hierarchies. We focussed on one such context by investigating whether bonobos socially learned others' arbitrary food preferences through mere observation. To this end, we trained two demonstrators to prefer or avoid distinctly

coloured food items, treated with either a sweet or bitter agent. Demonstrators then displayed their newly acquired preferences in front of naïve subjects. In subsequent choice tests, subjects generally matched their choices to the demonstrators' preferred food colours, despite having already tasted the equally palatable colour alternative. Both age and exposure to demonstrator preference had a significant positive effect on the proportion of matched choices. Moreover, in a context where errors can be costly, social learning was instant insofar as six of seven subjects used socially learned information to influence their very first food choice. We discuss these findings in light of the current debate on the evolution of social learning in animals.

Keywords: cognition; foraging; nonhuman primate; novel food; *Pan paniscus*; social learning

1. Introduction

Over the past decades, social learning has become a major topic in the field of comparative cognition (Whiten and van de Waal, 2018). Social learning, or more specifically "learning that is influenced by observation of, or interaction with, another animal (typically a conspecific) or its products" (Heyes, 1994) can be highly adaptive as it allows individuals to avoid costly trial-and-error learning, saving both time and energy and avoiding dangerous mistakes (Hopper et al., 2011). Furthermore, social learning can favour the rapid spread of advantageous behavioural innovations and, as such, acts as a 'second inheritance system' in addition to phylogenetically acquired behavioural traits (Whiten, 2005). Social learning is likely to be adaptive in many domains, including foraging, mate choice or predator avoidance (Galef and Giraldeau, 2001; Galef and Laland, 2005) and can even take place between species. Indeed, within a given ecological niche, different species are likely to be faced with the same requirements and constraints, as such, information acquired from heterospecifics

53 can be just as valuable as that acquired from conspecifics (Avarguès-Weber et al., 2013). For
54 example, the existing literature documents cases of interspecific social learning of food
55 source location in insects (Dawson and Chittka, 2012) and fish (Coolen et al., 2003), of
56 predator recognition and avoidance in mammals (Kitchen et al., 2010; Zuberbühler, 2000)
57 and reptiles (Vitousek et al., 2007) and of nesting site preference in birds (Seppänen and
58 Forsman, 2007). The importance of social learning is particularly relevant for young and
59 naïve individuals, who can avoid costly or maladaptive behaviour by observing and learning
60 from more experienced and older individuals that have, essentially, survived to adulthood in a
61 given environment (Galef and Laland, 2005).
62
63 Over the years, substantial efforts have been made to investigate the mechanisms underlying
64 social learning across different groups of animals, using both observational and experimental
65 techniques in the wild (e.g. apes: Hobaiter et al., 2014; monkeys: Kawai, 1965; birds: Aplin
66 et al., 2014) and in captivity (e.g. apes: Clay and Tennie, 2018; Dindo et al., 2011; Whiten et
67 al., 2005; monkeys: Dindo et al., 2008; van de Waal et al., 2013b; lemurs: Stoinski et al.,
68 2011; birds: Auersperg et al., 2014; see Reader and Biro, 2010 for a non-exhaustive survey).
69 A common approach to study social learning processes has been to use paradigms that
70 require manipulation of a container ('puzzle box') to extract an edible reward. A particularly
71 successful variant is the 'artificial fruit' (Whiten et al., 1996), which can be opened through
72 various means (e.g. lifting or sliding a door) to obtain a reward within. Such experiments
73 have brought to light not only evidence of social learning (e.g. van de Waal et al., 2010,
74 2013b) and social diffusion (e.g. Dindo et al., 2008, 2011; Whiten and Mesoudi, 2008) but
75 also of social conformity in animals (e.g. Dindo et al., 2009; Whiten et al., 2005). Overall,
76 these findings have broad implications for theories of the evolution of culture (see Whiten

77 and van de Waal, 2016a for a review) as they begin to unravel the basic building blocks for
78 the human capacity for culture, many of which are shared with non-human primates.
79
80 Another particularly common experimental paradigm in the laboratory is to expose subjects
81 to inaccessible food rewards that can only be accessed using a tool (e.g. Call and Tomasello,
82 1994; Horner and Whiten, 2005). However, while tool use is taxonomically widespread, it is
83 generally rare in most primate and non-primate species (Hunt et al., 2013), raising questions
84 on the extent to which experimental paradigms based on tool use are adequate to investigate
85 social learning capacities in such species. Most primates are capable of rich arrays of
86 manipulations, such as twisting, pulling, or peeling, but these manipulations tend to be
87 structurally simple (but see Byrne et al., 2001) and rarely involve tool use. Moreover,
88 although some chimpanzee communities have well established tool traditions (Visalberghi et
89 al., 2015) others only rarely use tools (Lamon et al., 2017; Lamon and Zuberbühler, 2015;
90 Reynolds, 2005), and tool use is curiously absent in wild bonobos (Koops et al., 2015) and
91 many other primate species. However, although social learning may give naïve observers an
92 advantage in some types of problem solving such as moss-sponging in chimpanzees
93 (Hobaiter et al., 2014) and nut-cracking in tufted capuchins (Coelho et al., 2015) and
94 chimpanzees (Marshall-Pescini and Whiten, 2008), and although this capacity for tool use
95 may translate into fitness consequences in certain contexts, for example, by providing highly
96 nutritional foods when usual food resources are scarce (Yamakoshi, 1998), tool use may not
97 be as significant for survival as general foraging strategies.
98
99 Social learning, in other words, may be better investigated in relation to more universally
100 ecologically relevant challenges, such as learning how to interact with socially powerful
101 group members or neighbouring groups or learning how to identify animal species that can

102 pose a predatory threat. Indeed, a recent study has revealed that chimpanzees learn rapidly
103 from each other how to react to humans, a major predator of chimpanzees (Samuni et al.,
104 2014). Regarding more ecologically relevant generalised foraging strategies, one of the key
105 domains for social learning is to discriminate edible from noxious foods (van de Waal et al.,
106 2014, 2013a). Although neophobia is clearly adaptive when encountering novel foods
107 (Addessi et al., 2005), it exposes individuals to starvation when environmental conditions
108 become unstable. A more adaptive strategy may be to follow a 'copy-when-uncertain'
109 strategy when relying on individual learning alone is risky (Laland, 2004). Evidence of social
110 learning of food choice has been brought to light in several bird species (e.g. house sparrows:
111 Fryday and Greig-Smith, 1994; red-winged blackbirds: Mason and Reidinger, 1981) but also
112 in primates, where food-related social learning is influenced by a number of factors. These
113 include sex, rank, age and association (Coussi-Korbel and Fragaszy, 1995) and while in some
114 species ingestion of novel foods is facilitated by the mere presence of conspecifics, regardless
115 of what they eat (e.g. tufted capuchin: Addessi and Visalberghi, 2001; chimpanzee: Finestone
116 et al., 2014), in others, individuals appear to learn something about the palatability of foods
117 by observing others (e.g. cotton-top tamarin: Snowdon and Boe, 2003; vervet monkey: van
118 de Waal et al., 2013a). Acquisition of such social information may be permitted by simple
119 social learning processes such as stimulus or local enhancement (Whiten and van de Waal,
120 2018).
121
122 One important factor in primate social learning of foraging behaviour is the attention that
123 young and naïve individuals pay to adult behaviour (Rapaport and Brown, 2008). Immature
124 individuals often wait for more experienced individuals to begin foraging before following
125 suit with the same food (e.g. Tarnaud, 2004; Whitehead, 1986; reviewed by Rapaport and
126 Brown, 2008). In apes, adult chimpanzees show more caution and close observation of

127 conspecific food-handling when presented with novel foods than familiar ones (Gustafsson et
128 al., 2014). Infant apes are very attentive to their mothers during foraging and show high rates
129 of co-feeding (Jaeggi et al., 2010; Rapaport and Brown, 2008; Ueno and Matsuzawa, 2005).
130 Food sharing and co-feeding between mother and offspring seem to provide infants with
131 direct learning opportunities and has been observed in lowland gorillas, orangutans,
132 chimpanzees and bonobos (see Rapaport and Brown, 2008 for review). Interestingly, this
133 effect can be so strong that in orangutans, for example, the diet differences between mothers
134 is larger than between mothers and their offspring (Jaeggi et al., 2010). Despite these
135 considerations, individual learning remains an important mechanism for acquiring food
136 aversion (e.g. pigtail macaques, spider monkeys, Fairbanks, 1975; tufted capuchins,
137 Visalberghi and Addessi, 2000) or complex forms of food processing (e.g. nettle feeding in
138 gorillas, Tennie et al., 2008). Some feeding behaviours are even thought to be part of species-
139 specific behavioural repertoires (e.g. rough-leaf swallowing in chimpanzees and bonobos,
140 Menzel et al., 2013) although social influences likely aid the spread of such behaviours
141 (Huffman and Hirata, 2004). Following an initial phase in which young primates
142 preferentially learn from their mothers, their pool of accessible information broadens as their
143 social learning strategies evolve and they begin to learn from other group members (Whiten
144 and van de Waal, 2018).
145
146 When these strategies lead to learning from other group members, then selectiveness for
147 specific models can become apparent. In a recent review, Whiten and van de Waal (2018)
148 presented four selective learning biases evidenced in primates when they learn from other
149 group members. Namely, bias for ‘knowledgeable’ or ‘expert’ models; for older models, for
150 models of a specific sex or for conformity (i.e., copying a behaviour expressed by a majority
151 of one’s group). Indeed, a general finding in empirical work on social learning in primates

highlights the importance of the seeding demonstrator's identity. Chimpanzees, for example, show a clear bias for copying older, higher-ranking and more knowledgeable individuals (Biro et al., 2003; Kendal et al., 2015). However, low ranking individuals may be just as effective in seeding novel behaviours when there is no 'model competition' (i.e., when there are no older or higher ranking individuals acting as demonstrator) (Watson et al., 2017). Yet, in a recent field study with chimpanzees, a novel behaviour, 'moss-sponging' invented by the alpha male, was shown to spread through the community via two transmission patterns. Initial spreading was within a spatio-temporal, proximity-based cohort but then mainly through the matrilines (Lamon et al., 2017), a pattern not previously reported in captive groups. The study thus indicated considerable flexibility of behaviour transmission patterns in chimpanzees. Indeed, in recent years, evidence for the flexible use of social learning strategies (i.e., what, when and whom to copy) has been found in several species spanning across taxa, from fish and birds to rats and primates (see Kendal et al., 2018; and Rendell et al., 2011 for reviews). This flexible use of social learning strategies is reflected in changes linked to ontogeny, experience, state and context (Kendal et al., 2018) and is likely an important factor as individuals enter the third phase of social learning proposed by Whiten and van de Waal (2018), which occurs when individuals migrate to new groups and are confronted with new locations and populations. For example, in an experiment in the wild, migrating male vervet monkeys abandoned their personal food preferences to adopt an opposite preference shown by their new group, which has been interpreted as potent social learning with a conformist bias (van de Waal et al., 2013a; Whiten and van de Waal, 2016b).

In the midst of these potential strategies for social learning, we were interested in experimentally assessing social learning in bonobos, in a universally ecologically relevant situation, i.e., food choice. In the present study we tested whether bonobos are able to

177 socially learn the arbitrary food preferences of a group member acting as demonstrator
178 through mere observation and whether they would adopt and maintain such preference
179 regardless of their own knowledge that both options were equally palatable. To achieve this
180 we ran a social learning experiment comprising of a series of experimental blocks in which
181 subjects observed two demonstrators consistently choosing food items of one novel colour
182 over another. Subjects were then tested to find out whether they preferred to choose food of
183 the same colour as the demonstrator. We predicted that, if subjects observed demonstrators
184 exhibiting a clear choice bias for one novel food colour over another, they would match this
185 bias above chance level in subsequent choice tests. As subjects had no prior experience with
186 these artificially coloured foods, we predicted social learning to be particularly strong during
187 the first experimental block when subjects were still naïve relative to these foods. We were
188 also interested in whether subjects were prepared to maintain such socially learned food
189 preferences, even after having experienced the respective colour alternatives.

190 **2. Methods**

191 *2.1 Ethical Note*

192 The study was authorised and ethically approved by the management of "La Vallée des
193 Singes". Although two individuals were regularly isolated for short periods of time (<30 min)
194 during this study, they were specifically selected based on their propensity to choose isolation
195 from the group on occasion thus avoiding stress for both the isolated individuals and the
196 group as a whole. The keeper isolated the individuals using methods regularly used on the
197 group when encouraging individuals to pass from one cage to another. When stress was
198 detected within the group, testing was postponed. The study was in line with
199 recommendations in the ARRIVE guidelines, and Animal Behaviour (1992) as well as the
200 EAZA and the AFdPZ code of ethics.

2.2 Study Site and Subjects

The experiment took place between February and November 2014 at La Vallée des Singes primate park, Romagne (France). Study subjects were selected from a large group of captive-born bonobos (N = 17, 8 males and 9 females, age range: 14 months - 45 years, mean = 15.2 years, see table 1), housed in a large indoor enclosure (400m^2) with access to two outdoor wooded islands covering 11,500m^2 in total.

Table 1. Study subjects housed at La Vallée des Singes and role in the experiment

Individual	Sex	Birth year	Age-class	Role
Diwani (DW)	M	1996	Adult	Demonstrator
Kelele (KEL)*	M	2004	Adult	Demonstrator
Ulindi (UL)	F	1993	Adult	Observer
Lingala (LNG)	F	2003	Sub-adult	Observer
Lucy (LY)	F	2003	Sub-adult	Observer
Nakala (NK)*	F	2007	Juvenile	Observer
Loto (LO)	M	2009	Juvenile	Observer
Moko (MO)	M	2012	Infant	Observer
Khalessi (KLS)	F	2012	Infant	Observer

Individuals marked by an asterisk had the same father; age-class as defined by Kano (1984)

Two adult males, DW and KEL, were selected as demonstrators based on the ease with which they could be isolated without apparent signs of stress to any of the group members. Six experimental blocks were carried out, each consisting of a *Demonstrator Training phase* (DT) for the demonstrators, followed by a *Preference Demonstration phase* (PD) in front of the subjects and finally an *Observer Testing phase* (OT) in which subjects underwent repeated choice tests. Three of the six experimental blocks were in the pink condition (i.e., demonstrator preference was for pink courgette) and three in the blue condition (i.e.,

demonstrator preference was for blue egg, further details are specified below). Testing was dependent on the personal motivation of each individual to, first, observe the Preference Demonstrations (PD), and, second, participate in the food choice tests of the Observer Testing phase (OT). Therefore, only 7 individuals of the 17 group members (two males and five females, age range: 14 months to 20 years, mean = 7.4 years) participated in the experiment (see table 1). One individual (LNG) participated only in the three experimental blocks of the pink condition, again, due motivational reasons. The remaining six individuals completed all six experimental blocks.

2.3 Experimental Design

We carried out six consecutive experimental blocks, three for the pink condition (P1, P2, P3) and three for the blue condition (B1, B2, B3) (fig. 1). Each experimental block consisted of three distinct phases: (1) Demonstrator Training phase (DT): demonstrators were given the choice between two artificially coloured foods (pink or blue) one of which was rendered unpalatable; (2) Preference Demonstration phase (PD): subjects observed demonstrators choosing their preferred food colours from a distance ranging from approximately 180 cm, across the corridor, to 500 cm on nearby structures or tunnels; (3) Observer Testing phase (OT) : subjects were given the choice between palatable pink or blue food (courgette or egg, see fig 1). For detailed explanations see below. In the pink condition (blocks P1, P2 and P3) demonstrator(s) were presented with pink and blue courgette, and demonstrator preference was for pink courgette. In the blue condition (blocks B1, B2 and B3) the demonstrator was presented with pink and blue egg and demonstrator preference was for blue egg.

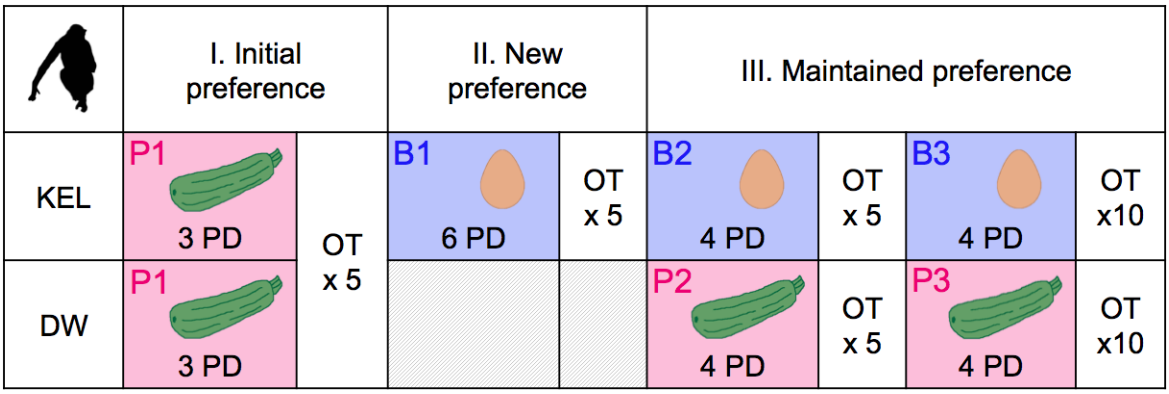


Figure 1. Experimental design - Experimental block order, demonstrator(s) identity, number of Preference Demonstration (PD) days, food used and preferred colour as well as number of Observer Test trials (OT) following each Preference Demonstration phase (PD). Each experimental block began with a Demonstrator Training phase (DT) consisting of 10 food presentations each, not represented on this figure. Testing period for each experimental block in chronological order: P1: Feb, B1: Jul, B2: Aug, B3: Sep, P2: Nov, P3: Nov.

2.3.1 Demonstrator Training Phase (DT)

In the initial Demonstrator Training phase (DT) for the first experimental block (P1), the two demonstrators, DW and KEL, learned that pink courgette was palatable (artificially sweetened), whereas blue courgette was unpalatable (artificially made bitter). In the three following experimental blocks (B1, B2, B3), KEL then learned the reverse colour pattern, albeit with a different food type (i.e., egg). Training for this new preference was achieved by presenting palatable blue egg, and unpalatable pink egg. Finally, in the last two experimental blocks (P2, P3) DW was provided with refresher training for a maintained preference for pink over blue courgette. In total, DW underwent 30 trials of food preference training with the pink courgette, while KEL underwent 10 with the pink courgette and 30 with the blue egg. To this end, at the start of each experimental block, the demonstrators were visually isolated from the rest of the group (Fig. 2a – cage 8, location marked DT) and were offered the choice between the pink and blue food (courgette or egg depending on the experimental block, see fig. 1 for details), one sweet, one bitter. Food presentation lasted 10 seconds after a first choice had been made. The first choice was defined as the first food touched, although in all

cases this was also the first food item eaten. Both individuals were given the choice 10 times, although we found that the colour-taste association was learned after just one experience with the bitter food. From the next trial onwards, both individuals consistently chose the sweet colour first and either ignored or only cautiously tasted and discarded the bitter colour second. Demonstrator Training (DT) was recorded using a PANASONIC HC-V727 full HD camera equipped with a SENNHEISER MKE 400 external microphone.

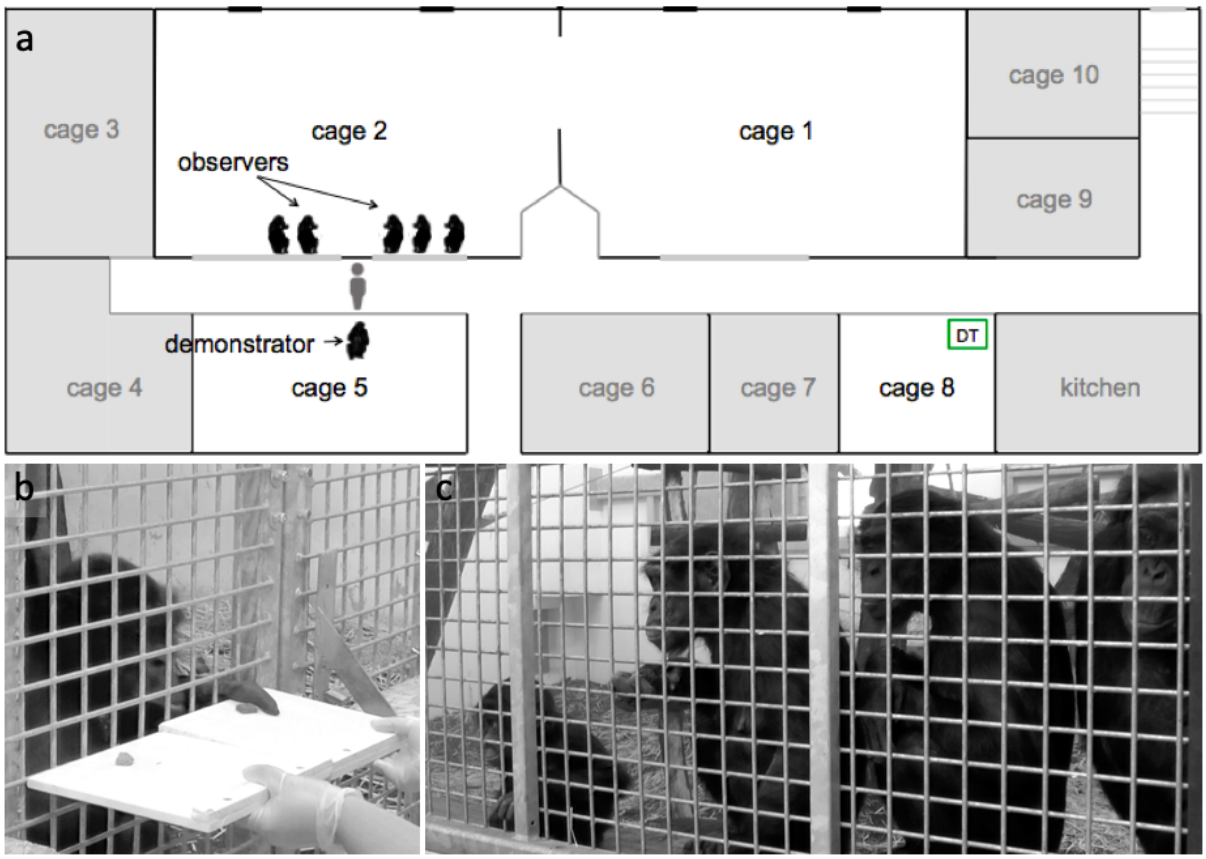


Figure 2. Experimental setup for social learning experiment – a) The Preference Demonstration phase (PD) is illustrated showing the demonstrator in cage 5 and the observers across the corridor in cage 2. DT marks the location used in cage 8 for the Demonstrator Training phase; b) Demonstrator choice, manual food presentation using 20 x 20 cm white plastic trays; c) Observers watching a Preference Demonstration (PD) from cage 2.

2.3.2 Preference Demonstration Phase (PD)

Following the Demonstrator Training phase (DT), a demonstrator was isolated and given the choice between the pink and blue food (Fig. 2b), while the rest of the group observed his choices from the opposite cage (Fig. 2a - cages 5 and 2 and fig. 2c). Demonstrators were allowed to choose 10 times. Food presentation lasted 10 seconds after a first choice had been made, so that observers could see more clearly which food had been chosen and which had been rejected. Preference Demonstrations (PD) were carried out once a day over several consecutive days (see fig. 1 for details).

We first ran experimental block P1, in which both DW and KEL were demonstrators and both showed a clear preference for the pink courgette. We chose to start with both demonstrators showing the same preference to increase the salience and strength of the demonstrated preference for the observers. Once established, we proceeded to experimental block B1 in which KEL was sole demonstrator and his colour preference was switched, albeit with a novel food type, so that his preference was for blue egg. We then continued in the blue condition with experimental blocks B2 and B3, again with KEL demonstrating his preference for blue egg. Finally, we carried out experimental blocks P2 and P3, with DW demonstrating his maintained preference for the pink courgette (see fig. 1). The number of demonstration days varied among experimental blocks (i.e. three consecutive demonstration days for each demonstrator in P1, six consecutive days for the sole demonstrator in B1 and four consecutive demonstration days for the sole demonstrator in B2, B3, P2 and P3 resulting in N=170 observable food choices for KEL and N=110 observable food choices for DW in total, see fig. 1).

297 During the Preference Demonstration phase (PD) both the demonstrators and the observers
298 where filmed in order to record both demonstrator colour choice and the number of trials
299 attended to by each observer (demonstrator: PANASONIC HC-V727 full HD camera
300 equipped with a SENNHEISER MKE 400 external microphone; observers: PANASONIC
301 HC-V100 full HD and PANASONIC HC-V727 full HD cameras). Subject attention to
302 demonstrator food choice (i.e., defined as the subject's head and eyes oriented towards the
303 demonstrator whilst the choice was made, regardless of posture) was coded post-hoc by GS
304 from the video footage and from oral commentaries recorded during the demonstrations.
305 Subject attention for a given trial was coded conservatively as either '1' or '0' (i.e., 1 =
306 observing, 0 = not observing). Individuals observing from outside the camera range were
307 recorded with help from a trained animal keeper.

308 *2.3.3 Observer Testing Phase (OT)*

309 Following the Preference Demonstration phase (PD) for each experimental block, observers
310 underwent individual preference testing in which sweetened pink and blue foods (courgette
311 or egg) were presented to them simultaneously. For the Observer Testing phase (OT), both
312 food types were prepared in the same way, but liquid sugarcane was used for all food to rule
313 out any possibility of odour cue-based choices by the observers. Food presentation ended as
314 soon as a choice had been made and was carried out opportunistically on all participating
315 observers (N=7) in all of the indoor cages and the outdoor enclosure.
316
317 Observers were tested five times each in blocks P1, P2, B1 and B2, and 10 times each in
318 blocks P3 and B3. Testing was opportunistic but no two consecutive tests were carried out on
319 a given individual unless the individual had resumed another activity before being retested. In
320 order to avoid feeding competition with other group members, the default protocol was to test

subjects in the absence of other group members. It was, however, unavoidable that some subjects (5 of 7) witnessed at least one choice test of another subject. In terms of their overall exposure, this was an insignificantly small proportion with far less influence than the Preference Demonstrations (PD) observed (see supplementary material, table S1). Testing was carried out over two or three consecutive days following the Preference Demonstration phase (PD) and was filmed using a PANASONIC HC-V100 full HD camera in order to record the colour chosen. As choices were always unambiguous and clear, we did not carry out any inter-observer reliability tests.

2.4 Food Preparation and Presentation

Two food types, raw courgettes and cooked egg whites (hereafter 'egg'), were used throughout the experiment. Individuals were familiar with the natural taste of these foods. For all members of the group, courgette is a lesser-valued food; egg is highly valued, but only familiar as hard-boiled and in the shell. For the first two phases of a given experimental block (i.e., Demonstrator Training (DT) and Preference Demonstration (PD)), the two food types were altered in taste and colour to obtain sweet pink courgette and bitter blue courgette for the pink condition, and sweet blue egg and bitter pink egg for the blue condition. We alternated the colour associated with the palatable food to control for any natural colour bias. The courgette was sliced and quartered (size approximately 2 x 2 x 0.5 cm) before being soaked overnight in either pink food colouring and a sweet additive (liquid sugarcane), or blue food colouring and a bitter additive (Bitrex® aqueous solution 2.5%, 0.2ml per 5cl of water: 100ppm). For the egg, either blue food colouring and a sweet additive or pink food colouring and a bitter additive were added before cooking the mixture in a microwave oven and cutting it into small pieces (approximately 2 x 2 x 0.5 cm). For the Observer Testing phase (OT) the two food types were altered in taste and colour to obtain only sweet pink and

345 blue foods and no bitter foods. Pink and blue food colouring where selected as few to no
346 foods of these colours are included in the group's regular diet. We chose not to carry out a
347 control for a natural colour bias as doing so would have provided the subjects with unwanted
348 experience with the two food colours.
349
350 To determine preferred food choice, items were offered manually. To this end, the
351 experimenter (GS) placed a cube of each colour of a given food type on two identical white
352 plastic trays (20 x 20 cm), which were placed, side by side, against the bars of the cages
353 allowing the individual to reach for the food using either the fingers or lips (Fig. 2b). The
354 position (left or right) of the different coloured food items was balanced and pseudo-
355 randomised, insofar as no given colour was presented on the same side for no more than three
356 consecutive trials.

357 *2.5 Statistical Analyses*

358 Statistical analyses were carried out using R 3.1.2., GUI 1.65 and SPSS version 22. Datasets
359 are available online [https://doi.org/10.17632/tczyxb9wvh.1]. Wilcoxon exact sign rank tests
360 were used to test comparisons between: 1) Subject attention to the two demonstrators (i.e.,
361 the percentage of DW and KEL Preference Demonstration (PD) trials observed by each
362 subject); 2) Performance in the first choice test, (i.e. number of matched and non-matched
363 choices made in the first test following each Preference Demonstration (PD)). For the overall
364 performance (i.e., the number of matched and non-matched choices made by each subject
365 overall), we ran a Generalised linear model with a quasi-binomial error structure. We
366 modelled the probability of making matched choice across all trials per individual as a
367 function of age and proportion of observed Preference Demonstration (PD) trials.

3. Results

3.1 Preference Demonstration Phase (PD)

3.1.1 Demonstrator performance

KEL and DW's performance during Preference Demonstrations (PD) was close to perfect. They chose the correct colour first in 97% and 99% of trials and ate the correct colour exclusively in 95% and 96% of trials, respectively (i.e. pink courgette in P1, P2 and P3 and blue egg in B1, B2 and B3; KEL N=170 and DW N=110, see Preference Demonstration phase (PD) in methods for details).

3.1.2 Attention to demonstrators

While observers paid more attention to Preference Demonstrations (PD) by DW than to those by KEL, the difference was not statistically significant (mean percentage of demonstrations watched by the subjects: DW 35.4%, KEL 29.8%, Wilcoxon exact test, Z = -1.014, N = 7, exact $P = 0.38$, two-tailed).

3.2 Observer Testing Phase (OT)

3.2.1 First choice performance

For the first trial of the first experimental block (P1) all observers were naïve having had no personal experience with the artificially altered foods. Nevertheless, six of seven subjects chose the colour chosen by the demonstrator in this first trial. When analysing first choices across all experimental blocks, individuals chose the matched colour significantly more often than the non-matched colour (Z = -2.64, N = 6, $P = 0.031$, two-tailed, Wilcoxon exact test; Fig. 3; one subject, LNG, could not be included in this analysis as she partook in only 3 of the 6 experimental blocks). Of the seven subjects, six chose mostly the matched colour as

their first choice for each experimental block, and only one chose the matched and non-matched colour equally, suggesting that, as per our predictions, individuals immediately experienced a significant bias towards the foods chosen by the demonstrators, a clear demonstration of rapid social learning by observation.

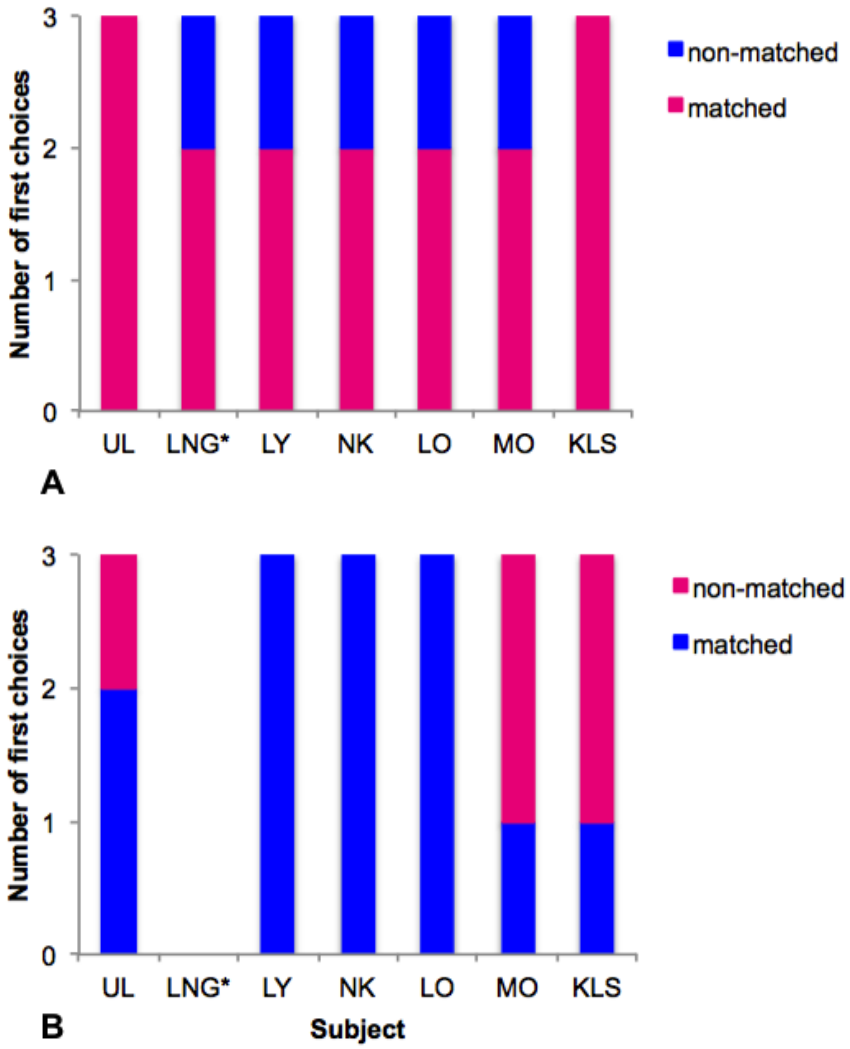


Figure 3. Number of matched and non-matched colour choices for each subject in the first choice test of the Observer Testing phase (OT): A) pink experimental blocks (P1, P2, P3), B) blue experimental blocks (B1, B2, B3), subjects classed by decreasing age from left to right.

400 *3.2.2 Overall performance*

401 Taking into account the observers' overall performance in choosing the matched colour,
402 results show that the food preference of the demonstrators continued to have an influence on
403 observer colour choice. Indeed, the model supported the fact that subjects matched their
404 choices to those of the demonstrators significantly above chance levels (see table 2 and figure
405 4 for raw data).

406

407 **Table 2.** Results of the logistic regression modelling the proportion of matched trials (N = 7).

	Estimate	Standard error	Z value	P
Intercept	0.64	0.09	6.85	0.002 ***
Age	7.33	1.60	4.59	0.010 *
Proportion of trials observed	1.65	0.50	3.32	0.029 *

408 Estimates are on a logit scale.

409 This is important because, over the course of the experiment, all observers occasionally tasted
410 the alternative colour choice (i.e., unmatched choice), which was identical in taste and
411 palatability to the matched choice (both treated with liquid sugarcane). Nonetheless, they
412 chose the food colour preferred by the demonstrators more than the alternative.

413

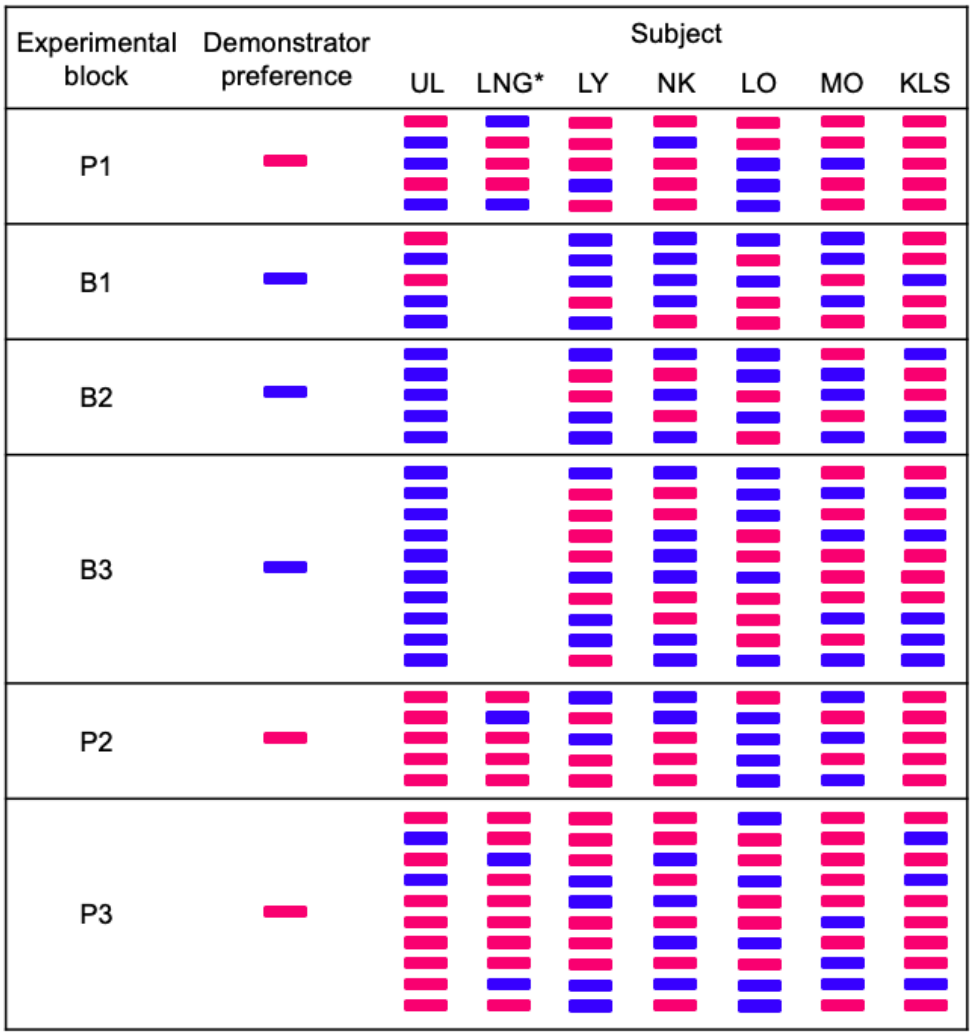
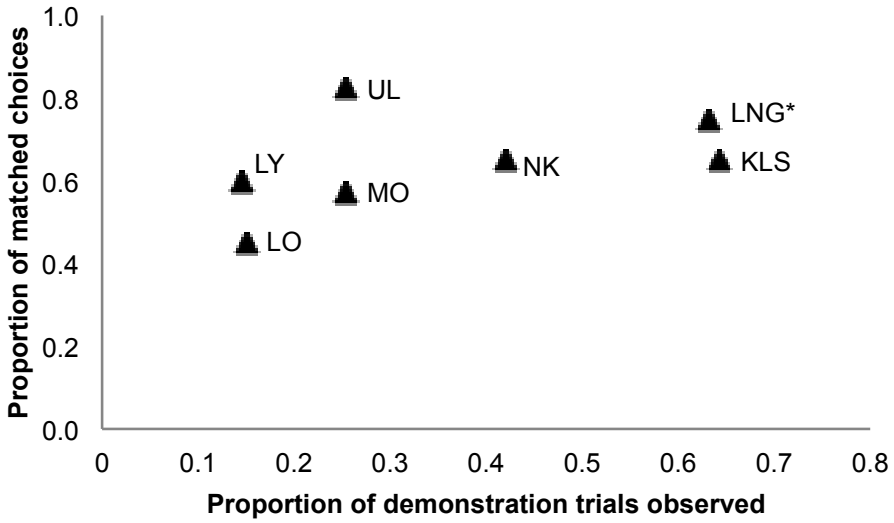


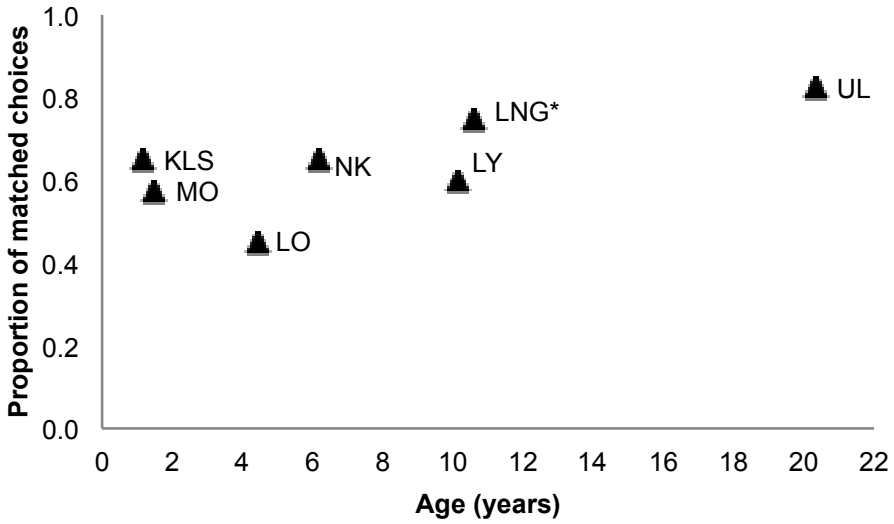
Figure 4. Experimental block, demonstrator preference and all subject choices during the Observer Testing phase (OT) for all six experimental blocks (both subject choice trials and experimental blocks are shown in chronological order).

Furthermore, both age and proportion of trials observed had a significant positive effect on the proportion of matched choices (Table 2, Figs. 5 and 6).



421

422 **Figure 5.** Proportion of matched choices made during Observer Testing phase (OT) and proportion
423 of Preference Demonstration (PD) trials observed by each subject. LNG, marked by an asterisk,
424 participated in only P1, P2 & P3.



425

426 **Figure 6.** Proportion of matched choices made during the Observer Testing phase (OT) and subject
427 age in years. LNG, marked by an asterisk, participated in only P1, P2 & P3.

428

429 When considering individual performance (i.e. percentage of matched choices during the
430 Observer Testing phase (OT)), it can be noted that there is considerable inter-individual
431 variability (Table 3), variability which can be explained in part by the age of subjects and

their attention to Preference Demonstrations (PD) (as shown in the model). Nonetheless, six of seven subjects chose the matched food colour more often than the unmatched food colour.

Table 3. Individual performance over all six experimental blocks

Subject	*N*	Proportion of demonstration trials observed	Food colour choice matched : unmatched	Performance (% matched)
UL	40	0.25	33:7	82.5
LNG	20	0.63	15:5	75.0
LY	40	0.14	24:16	60.0
NK	40	0.42	26:14	65.0
LO	40	0.15	18:22	45.0
MO	40	0.25	23:17	57.5
KLS	40	0.64	26:14	65.0

Proportion of demonstration trials observed, number of matched and unmatched choices and percentage of matched choices made by subjects. One individual (LNG) participated in the Observer Testing phase (OT) for only three of the six experimental blocks: P1, P2 & P3.

4. Discussion

In this study we sought to investigate whether bonobos are capable of acquiring and retaining information relating to arbitrary food preferences of fellow group members through mere observation. In other words, can bonobos socially learn the different food preferences of other group members and do they abide to these even if doing so goes against their own experience and knowledge (i.e., despite knowing that both colour alternatives are equally palatable)? In our experiment, both demonstrators were exposed to trial-and-error learning to install an arbitrary preference for visually novel food items, which led immediately to a clear bias for the palatable food. In a series of six experimental blocks, subjects were then provided with the opportunity to observe demonstrator preferences before

449 being presented with the choice of two colour alternatives of an otherwise identical food
450 item. The results, as demonstrated by the number of matched choices made by the subjects
451 in the first choice of each experimental block, showed that the subjects had developed an
452 immediate preference for the food item chosen by the demonstrator, demonstrating rapid and
453 reliable social learning. Furthermore, and importantly, this effect occurred despite subjects
454 being exposed to a complex demonstration pattern during which one demonstrator (KEL)
455 demonstrated opposing colour preferences for different foods (see fig. 1). In this paradigm
456 which confronted the subjects with the question of "what to eat?" it is likely that the
457 mechanism at work is simple stimulus enhancement as is often the case with this and other
458 everyday behavioural questions such as "where to sleep?" or "who and what to beware of?"
459 (Whiten and van de Waal, 2018).

460

461 Our second finding relates to the fact that subjects' performance continued to be biased
462 towards the demonstrated preference, as indicated in the subjects' overall performance, even
463 after individuals had opportunities to taste the alternatively coloured foods (i.e., when both
464 coloured foods were known to be equally palatable, see fig. 4 for frequencies of alternative
465 colour choice throughout the experiment). We noted considerable inter-individual
466 differences in performance during the crucial Observer Testing phase (OT), which was at
467 least partially explained by subject age and exposure to Preference Demonstrations (PD)
468 (see fig. 5 and 6); indeed, younger individuals and those that observed only a few
469 demonstrations were less likely to match their choices to those of the demonstrators in the
470 Observer Testing phase (OT) than older individuals or those that observed many
471 demonstrations. It seems quite intuitive that performance should improve with increased
472 exposure to demonstrator preference, however, the result observed in relation to subject age
473 is in contradiction with the general finding that suggests that juvenile primates are more

474 prone to use social information than are adults (e.g. Coelho et al., 2015; Matsuzawa, 1994).
475 In the present study we found that older subjects were those most likely to match their
476 choices to those of the demonstrators.

477

478 When considering the possible explanations for subjects generally adhering to demonstrator
479 preferences we must consider the recent findings which have revealed that rather than being
480 set rules, social learning strategies are used flexibly at the individual, group and population
481 level (see Kendal et al., 2018 for a non-exhaustive review of theoretical and empirical
482 support for a broad range of social learning strategies), in fact a recent study in the wild has
483 demonstrated that this flexibility can even be at the species level (Bono et al., 2018). In their
484 review, Kendal et al. (2018) present a variety of strategies as to when, whom and what to
485 copy. In our study, following their initial choice, not only were subjects rapidly exposed to
486 the alternative colour choice, but in choosing the alternative colour they were immediately
487 rewarded, just as they were when copying the demonstrator. And yet in our study, subjects
488 generally adhered to the preference shown by the demonstrator. This propensity to adhere to
489 demonstrator preference might be in line with a 'when' learning strategy more expected of
490 naïve subjects: 'copy-when-uncertain'. This would suggest that subjects perceived
491 uncertainty during testing which increased their willingness to rely on social information
492 (Galef et al., 2008; Kendal et al., 2015) rather than their own experience. In some studies
493 with apes and human children subjects have been found to follow the demonstrator's strategy
494 even if this meant going against their own personal preference (e.g. human children, Gergely
495 et al., 2002; chimpanzees, Hopper et al., 2011) while in other studies this was not the case
496 (Vale et al., 2017). Vale and colleagues (2017), for instance, demonstrated that chimpanzees
497 preferred to rely on their personal experience with unpalatable foods rather than to conform
498 to group norms. Observation of group members eating the previously 'unpalatable' food did,

however, promote the re-exploration of that food through social learning. This pattern of relying more on one's own experience than on social information from conspecifics has also been observed in other animal species. For example, Fryday and Greig-Smith (1994), demonstrated that the amount of food consumed by house sparrows was influenced not by demonstrator consumption, but by their own previous experience with the food (i.e., palatable untreated food or unpalatable quinine-treated food).

Regarding a possible "who" strategy, there is much empirical work to support model-based biases, for instance the propensity to learn from older and higher ranking group members (e.g. Biro et al., 2003; Kendal et al., 2015). In our study, the two demonstrators were not the highest ranking male in the group, nor were they the oldest, and neither one was directly related to any of the subjects, nevertheless social learning took place, as shown, for example, by the results obtained for UL, a high-ranking adult female, who was most strongly influenced by these males (i.e., UL made the highest number of matched choices of all subjects, see table 3 and fig. 4). This result may be indicative of a 'who' bias for 'knowledgeable' or 'expert' models (Whiten and van de Waal, 2018) or perhaps, similarly to chimpanzees, in the absence of 'demonstrator-competition' (i.e., the presence of the usually more favoured, older and higher-ranking demonstrators), low-ranking individuals are able to successfully seed a behaviour (Watson et al., 2017). This finding is thus at odds with one of de Waal's (2001) bonding- and identification-based observational learning model predictions, which is that, for social learning to take place, demonstrators ought to be high ranking individuals, a pattern that has been found in both captive (Horner et al., 2010) and wild chimpanzees (Hobaiter et al., 2014) although kin-based learning may be more important in establishing long-term behavioural traditions (Lamon et al., 2017).

523 Kendal et al. further present a set of frequency-dependant biases. Indeed, potential
524 explanation for subjects adhering to demonstrator preference, despite possessing the
525 knowledge that both foods were equally palatable, might come from some sort of desire to
526 conform (as predicted by de Waal's (2001) BIOL model, although the author predicted a
527 desire to conform specifically to higher ranking and older individuals), perhaps for the sake
528 of social cohesion (Hopper et al., 2011). In humans, this effect is particularly strong if a novel
529 behaviour is shown by several or a majority of group members. Conformity predicts that
530 individuals will change their own behaviour and adopt the majority behaviour in order to
531 comply with what they perceive as 'social norms' (van Leeuwen and Haun, 2014). Whether
532 or not such social influence really requires a majority (e.g. Asch, 1956) or comes into play
533 even when the behaviour has initially been demonstrated by a minority, is often unclear
534 (Hopper et al., 2011; but see Cialdini and Trost, 1984 for a review). In our study we did not
535 test specifically for conformity, since subjects did not have to adhere to the behaviour of a
536 majority, instead we demonstrated that several group members adopted the same preference
537 (non-exclusively) as that expressed by the two demonstrators, and this was despite having
538 knowledge that both foods were equally palatable.
539
540 Another explanation is that subjects were following a sensible survival strategy: if a
541 demonstrator systematically refuses to eat a certain food, then it may be reasonable to assume
542 that he does so for a good reason. In the present case, following the demonstrator's choice
543 and following a 'better-safe-than-sorry' strategy was cost free. The underlying drivers of such
544 behaviour open questions for future research.

5. Conclusion

We conclude that, even in the absence of olfactory and taste cues, bonobos are able to acquire and memorise others' food preferences and are prepared to adhere to them, even when the demonstrator is not a high ranking individual. Bonobos, similar to humans, are susceptible to acquiring information from watching the behaviour of others even if demonstrators are socially unimportant and even adhere to these learned behaviours despite personal knowledge that there is no additional reward in doing so. Furthermore, while this study does not allow us to draw conclusions regarding the exact social learning mechanism(s) at work, the results, even if due to simple stimulus enhancement, as has been suggested for social learning of many of the day-to-day behaviours (Whiten and van de Waal, 2018), demonstrate that subjects matched their choices to those of the demonstrators regardless of the colour, food type and demonstrator identity. We believe this supports not only the fact that learning from others in the context of food acquisition is of paramount importance but also provides further support to the ongoing discussion around the flexible use of social learning strategies.

Finally, it is important to point out that our findings were made in the context of an ecologically important situation, i.e. learning about novel foods, which highlights the fact that social learning theory is likely to benefit from paradigms that focus on more universal ecologically relevant problems.

Acknowledgements

The research leading to these results has received funding from the European Research Council under the European Union's Seventh Framework Programme (FP7/2007-2013) / ERC grant agreement n°283871 and the Swiss National Science Foundation (Social learning in primate communication: 31003A_166458 / Coordinating joint action in apes: Testing the

boundaries of the human interaction engine: CR31I3_159655). We thank “La Vallée des Singes” and its director, Emmanuel Le Grelle, as well as “Le Conservatoire pour la Conservation des Primates” for allowing access to the study site and subjects. We also thank keepers, Carole Michelet, Franck Alexieff, Jérémy Mergault, and Alexandre Albert for their valuable help in carrying out the experiment as well as Josep Call, Redouan Bshary and Christof Neumann for valuable discussion as well as Radu Slobodeanu for statistical advice.

Declarations of interest: none

References

Addessi, E., Galloway, A.T., Visalberghi, E., Birch, L.L., 2005. Specific social influences on the acceptance of novel foods in 2–5-year-old children. Appetite 45, 264–271. https://doi.org/10.1016/j.appet.2005.07.007

Addessi, E., Visalberghi, E., 2001. Social facilitation of eating novel food in tufted capuchin monkeys (Cebus apella): input provided by group members and responses affected in the observer. Animal Cognition 4, 297–303. https://doi.org/10.1007/s100710100113

Animal Behaviour, 1992. Guidelines for the use of animals in research. Animal Behaviour 43, 185–188.

Aplin, L.M., Farine, D.R., Morand-Ferron, J., Cockburn, A., Thornton, A., Sheldon, B.C., 2014. Experimentally induced innovations lead to persistent culture via conformity in wild birds. Nature 518, 538–541. https://doi.org/10.1038/nature13998

Asch, S.E., 1956. Studies of independance and conformity: I. A minority of one against a unanimous majority. Psychological Monographs 70, 1–70.

Auersperg, A.M.I., von Bayern, A.M.I., Weber, S., Szabadvari, A., Bugnyar, T., Kacelnik, A., 2014. Social transmission of tool use and tool manufacture in Goffin cockatoos (Cacatua goffini). Proceedings of the Royal Society B: Biological Sciences 281, 20140972. https://doi.org/10.1098/rspb.2014.0972

Avarguès-Weber, A., Dawson, E.H., Chittka, L., 2013. Mechanisms of social learning across species boundaries: Social learning across species boundaries. Journal of Zoology 290, 1–11. https://doi.org/10.1111/jzo.12015

Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., Matsuzawa, T., 2003. Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. Animal Cognition 6, 213–223. https://doi.org/10.1007/s10071-003-0183-x

Bono, A.E.J., Whiten, A., Van Schaik, C.P., Krützen, M., Eichenberger, F., Schnider, A., van de Waal, E., 2018. Payoff- and sex-biased social learning interact in a wild primate population. Current Biology 28, 2800-2805.e4. https://doi.org/10.1016/j.cub.2018.06.015

Byrne, R.W., Corp, N., Byrne, J.M.E., 2001. Estimating the complexity of animal behaviour: How mountain gorillas eat thistles. Behaviour 138, 525–557. https://doi.org/10.1163/156853901750382142

Call, J., Tomasello, M., 1994. The social learning of tool use by orangutans (Pongo pygmaeus). Human Evolution 9, 297–313.

Cialdini, R.B., Trost, M.R., 1984. Social influence: Social norms, conformity, and compliance, in: Gilbert, D.T., Fiske, S.T., Lindzey, G. (Eds.), The Handbook of Social Psychology. Oxford University Press, Oxford, pp. 151–192.

Clay, Z., Tennie, C., 2018. Is Overimitation a Uniquely Human Phenomenon? Insights From Human Children as Compared to Bonobos. Child Development 89, 1–10. https://doi.org/10.1111/cdev.12857

Coelho, C.G., Falótico, T., Izar, P., Mannu, M., Resende, B.D., Siqueira, J.O., Ottoni, E.B., 2015. Social learning strategies for nut-cracking by tufted capuchin monkeys (Sapajus spp.). Animal Cognition 18, 911–919. https://doi.org/10.1007/s10071-015-0861-5

Coolen, I., Bergen, Y.V., Day, R.L., Laland, K.N., 2003. Species difference in adaptive use of public information in sticklebacks. Proceedings of the Royal Society B: Biological Sciences 270, 2413–2419. https://doi.org/10.1098/rspb.2003.2525

621 Coussi-Korbel, S., Fragaszy, D.M., 1995. On the relation between social dynamics and social
622 learning.pdf. Animal Behaviour 50, 1441–1453.
623 Dawson, E.H., Chittka, L., 2012. Conspecific and Heterospecific Information Use in
624 Bumblebees. PLoS ONE 7, e31444. https://doi.org/10.1371/journal.pone.0031444
625 de Waal, F.B.M., 2001. The ape and the sushi master: Cultural reflections of a primatologist.
626 Basic Books, New York, NY.
627 Dindo, M., Stoinski, T., Whiten, A., 2011. Observational learning in orangutan cultural
628 transmission chains. Biol. Lett. 7, 181–183. https://doi.org/10.1098/rsbl.2010.0637
629 Dindo, M., Thierry, B., Whiten, A., 2008. Social diffusion of novel foraging methods in
630 brown capuchin monkeys (Cebus apella). Proceedings of the Royal Society B:
631 Biological Sciences 275, 187–193. https://doi.org/10.1098/rspb.2007.1318
632 Dindo, M., Whiten, A., de Waal, F.B.M., 2009. In-group conformity sustains different
633 foraging traditions in capuchin monkeys (Cebus apella). PLoS ONE 4, e7858.
634 https://doi.org/10.1371/journal.pone.0007858
635 Fairbanks, L., 1975. Communication of food quality in captive Macaca nemestrina and free-
636 ranging Ateles geoffroyi. Primates 16, 181–190.
637 Finestone, E., Bonnie, K.E., Hopper, L.M., Vreeman, V.M., Lonsdorf, E.V., Ross, S.R.,
638 2014. The interplay between individual, social, and environmental influences on
639 chimpanzee food choices. Behavioural Processes 105, 71–78.
640 https://doi.org/10.1016/j.beproc.2014.03.006
641 Fryday, S.L., Greig-Smith, P.W., 1994. The effects of social learning on the food choice of
642 the house sparrow (Passer domesticus). Behaviour 128, 281–300.
643 Galef, B.G., Dudley, K.E., Whiskin, E.E., 2008. Social learning of food preferences in
644 'dissatisfied' and 'uncertain' Norway rats. Animal Behaviour 75, 631–637.
645 https://doi.org/10.1016/j.anbehav.2007.06.024
646 Galef, B.G., Giraldeau, L.-A., 2001. Social influences on foraging in vertebrates: causal
647 mechanisms and adaptive functions. Animal Behaviour 61, 3–15.
648 https://doi.org/10.1006/anbe.2000.1557
649 Galef, B.G., Laland, K.N., 2005. Social learning in animals: empirical studies and theoretical
650 models. Bioscience 55, 489–499.
651 Gergely, G., Bekkering, H., Király, I., 2002. Developmental psychology: Rational imitation
652 in preverbal infants. Nature 415, 755–755.
653 Gustafsson, E., Saint Jalme, M., Bomsel, M.-C., Krief, S., 2014. Food Neophobia and Social
654 Learning Opportunities in Great Apes. International Journal of Primatology 35, 1037–
655 1071. https://doi.org/10.1007/s10764-014-9796-y
656 Heyes, C.M., 1994. Social learning in animals: categories and mechanisms. Biological
657 Reviews 69, 207–231.
658 Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W., Gruber, T., 2014. Social network
659 analysis shows direct evidence for social transmission of tool use in wild
660 chimpanzees. PLoS Biology 12, e1001960.
661 https://doi.org/10.1371/journal.pbio.1001960
662 Hopper, L.M., Schapiro, S.J., Lambeth, S.P., Brosnan, S.F., 2011. Chimpanzees' socially
663 maintained food preferences indicate both conservatism and conformity. Animal
664 Behaviour 81, 1195–1202. https://doi.org/10.1016/j.anbehav.2011.03.002
665 Horner, V., Proctor, D., Bonnie, K.E., Whiten, A., de Waal, F.B.M., 2010. Prestige affects
666 cultural learning in chimpanzees. PLoS ONE 5, e10625.
667 https://doi.org/10.1371/journal.pone.0010625
668 Horner, V., Whiten, A., 2005. Causal knowledge and imitation/emulation switching in
669 chimpanzees (Pan troglodytes) and children (Homo sapiens). Animal Cognition 8,
670 164–181. https://doi.org/10.1007/s10071-004-0239-6

671 Huffman, M.A., Hirata, S., 2004. An experimental study of leaf swallowing in captive
672 chimpanzees: insights into the origin of a self-medicative behavior and the role of
673 social learning. Primates 45, 113–118. https://doi.org/10.1007/s10329-003-0065-5
674 Hunt, G.R., Gray, R.D., Taylor, A.H., 2013. Why is tool use rare in animals?, in: Sanz, C.M.,
675 Call, J., Boesch, C. (Eds.), Tool Use in Animals: Cognition and Ecology. Cambridge
676 University Press, Cambridge, pp. 89–118.
677 Jaeggi, A.V., Dunkel, L.P., Van Noordwijk, M.A., Wich, S.A., Sura, A.A.L., Van Schaik,
678 C.P., 2010. Social learning of diet and foraging skills by wild immature Bornean
679 orangutans: implications for culture. American Journal of Primatology 72, 62–71.
680 https://doi.org/10.1002/ajp.20752
681 Kano, T., 1984. Distribution of pygmy chimpanzees (Pan paniscus) in the central Zaire basin.
682 Folia primatologica 43, 36–52.
683 Kawai, M., 1965. Newly-acquired pre-cultural behavior of the natural troop of Japanese
684 monkeys on Koshima Islet. Primates 6, 1–30.
685 Kendal, R., Hopper, L.M., Whiten, A., Brosnan, S.F., Lambeth, S.P., Schapiro, S.J., Hoppitt,
686 W., 2015. Chimpanzees copy dominant and knowledgeable individuals: implications
687 for cultural diversity. Evolution and Human Behavior 36, 65–72.
688 https://doi.org/10.1016/j.evolhumbehav.2014.09.002
689 Kendal, R.L., Boogert, N.J., Rendell, L., Laland, K.N., Webster, M., Jones, P.L., 2018. Social
690 Learning Strategies: Bridge-Building between Fields. Trends in Cognitive Sciences
691 22, 651–665. https://doi.org/10.1016/j.tics.2018.04.003
692 Kitchen, D.M., Bergman, T.J., Cheney, D.L., Nicholson, J.R., Seyfarth, R.M., 2010.
693 Comparing responses of four ungulate species to playbacks of baboon alarm calls.
694 Animal Cognition 13, 861–870. https://doi.org/10.1007/s10071-010-0334-9
695 Koops, K., Furuichi, T., Hashimoto, C., 2015. Chimpanzees and bonobos differ in intrinsic
696 motivation for tool use. Scientific Reports 5. https://doi.org/10.1038/srep11356
697 Laland, K.N., 2004. Social Learning Strategies. Learning and Behaviour 32, 4–14.
698 Lamon, N., Neumann, C., Gruber, T., Zuberbühler, K., 2017. Kin-based cultural transmission
699 of tool use in wild chimpanzees. Science Advances 3, e1602750.
700 Lamon, N., Zuberbühler, K., 2015. Object manipulation and tool use in wild chimpanzees of
701 the Budongo forest, Uganda. Folia Primatologica 86, 235–386.
702 https://doi.org/10.1159/000435825
703 Marshall-Pescini, S., Whiten, A., 2008. Social learning of nut-cracking behavior in East
704 African sanctuary-living chimpanzees (Pan troglodytes schweinfurthii). Journal of
705 Comparative Psychology 122, 186–194. https://doi.org/10.1037/0735-7036.122.2.186
706 Mason, J.R., Reidinger, R.F., 1981. Effects of social facilitation and observational learning
707 on feeding behaviour of the red-winged blackbird (Agelaius phoeniceus). The Auk
708 98, 778–784.
709 Matsuzawa, T., 1994. Field experiments on use of stone tools by chimpanzees in the wild, in:
710 Wrangham, R.W., McGrew, W.C., De Waal, F.B.M., Heltne, P.G. (Eds.),
711 Chimpanzee Cultures. Harvard University Press, Cambridge, MA, US, pp. 351–370.
712 Menzel, C., Fowler, A., Tennie, C., Call, J., 2013. Leaf Surface Roughness Elicits Leaf
713 Swallowing Behavior in Captive Chimpanzees (Pan troglodytes) and Bonobos (P.
714 paniscus), but not in Gorillas (Gorilla gorilla) or Orangutans (Pongo abelii).
715 International Journal of Primatology 34, 533–553. https://doi.org/10.1007/s10764-
716 013-9679-7
717 Rapaport, L.G., Brown, G.R., 2008. Social influences on foraging behavior in young
718 nonhuman primates: Learning what, where, and how to eat. Evolutionary
719 Anthropology: Issues, News, and Reviews 17, 189–201.
720 https://doi.org/10.1002/evan.20180

721 Reader, S.M., Biro, D., 2010. Experimental identification of social learning in wild animals.
722 Learning & Behavior 38, 265–283. https://doi.org/10.3758/LB.38.3.265
723 Rendell, L., Fogarty, L., Hoppitt, W.J.E., Morgan, T.J.H., Webster, M.M., Laland, K.N.,
724 2011. Cognitive culture: theoretical and empirical insights into social learning
725 strategies. Trends in Cognitive Sciences 15, 68–76.
726 https://doi.org/10.1016/j.tics.2010.12.002
727 Reynolds, V., 2005. The Chimpanzees of the Budongo Forest: Ecology, behaviour and
728 conservation. Oxford University Press, Oxford.
729 Samuni, L., Mundry, R., Terkel, J., Zuberbühler, K., Hobaiter, C., 2014. Socially learned
730 habituation to human observers in wild chimpanzees. Animal Cognition 17, 997–
731 1005. https://doi.org/10.1007/s10071-014-0731-6
732 Seppänen, J.-T., Forsman, J.T., 2007. Interspecific Social Learning: Novel Preference Can Be
733 Acquired from a Competing Species. Current Biology 17, 1248–1252.
734 https://doi.org/10.1016/j.cub.2007.06.034
735 Snowdon, C.T., Boe, C.Y., 2003. Social communication about unpalatable foods in tamarins
736 (Saguinus oedipus). Journal of Comparative Psychology 117, 142–148.
737 https://doi.org/10.1037/0735-7036.117.2.142
738 Stoinski, T.S., Drayton, L.A., Price, E.E., 2011. Evidence of social learning in black-and-
739 white ruffed lemurs (Varecia variegata). Biology Letters 7, 376–379.
740 https://doi.org/10.1098/rsbl.2010.1070
741 Tarnaud, L., 2004. Ontogeny of feeding behavior of Eulemur fulvus in the dry forest of
742 Mayotte. International Journal of Primatology 25, 803–824.
743 Tennie, C., Hedwig, D., Call, J., Tomasello, M., 2008. An experimental study of nettle
744 feeding in captive gorillas. American Journal of Primatology 70, 584–593.
745 https://doi.org/10.1002/ajp.20532
746 Ueno, A., Matsuzawa, T., 2005. Response to novel food in infant chimpanzees. Behavioural
747 Processes 68, 85–90. https://doi.org/10.1016/j.beproc.2004.09.002
748 Vale, G.L., Davis, S.J., van de Waal, E., Schapiro, S.J., Lambeth, S.P., Whiten, A., 2017.
749 Lack of conformity to new local dietary preferences in migrating captive
750 chimpanzees. Animal Behaviour 124, 135–144.
751 https://doi.org/10.1016/j.anbehav.2016.12.007
752 van de Waal, E., Borgeaud, C., Whiten, A., 2013a. Potent social learning and conformity
753 shape a wild primate's foraging decisions. Science 340, 483–485.
754 https://doi.org/10.1126/science.1232769
755 van de Waal, E., Bshary, R., Whiten, A., 2014. Wild vervet monkey infants acquire the food-
756 processing variants of their mothers. Animal Behaviour 90, 41–45.
757 https://doi.org/10.1016/j.anbehav.2014.01.015
758 van de Waal, E., Claidière, N., Whiten, A., 2013b. Social learning and spread of alternative
759 means of opening an artificial fruit in four groups of vervet monkeys. Animal
760 Behaviour 85, 71–76. https://doi.org/10.1016/j.anbehav.2012.10.008
761 van de Waal, E., Renevey, N., Favre, C.M., Bshary, R., 2010. Selective attention to
762 philopatric models causes directed social learning in wild vervet monkeys.
763 Proceedings of the Royal Society B: Biological Sciences 277, 2105–2111.
764 https://doi.org/10.1098/rspb.2009.2260
765 van Leeuwen, E.J.C., Haun, D.B.M., 2014. Conformity without majority? The case for
766 demarcating social from majority influences. Animal Behaviour 96, 187–194.
767 http://dx.doi.org/10.1016/j.anbehav.2014.08.004
768 Visalberghi, E., Addessi, E., 2000. Response to change in food palatability in tufted capuchin
769 monkeys, Cebu apella. Animal Behaviour 59, 231–238.

Visalberghi, E., Sirianni, G., Fragaszy, D., Boesch, C., 2015. Percussive tool use by Taï Western chimpanzees and Fazenda Boa Vista bearded capuchin monkeys: a comparison. Philosophical Transactions of the Royal Society B: Biological Sciences 370, 20140351. https://doi.org/10.1098/rstb.2014.0351

Vitousek, M.N., Adelman, J.S., Gregory, N.C., Clair, J.J.H.S., 2007. Heterospecific alarm call recognition in a non-vocal reptile. Biology Letters 3, 632–634. https://doi.org/10.1098/rsbl.2007.0443

Watson, S.K., Reamer, L.A., Mareno, M.C., Vale, G., Harrison, R.A., Lambeth, S.P., Schapiro, S.J., Whiten, A., 2017. Socially transmitted diffusion of a novel behavior from subordinate chimpanzees. American Journal of Primatology 79, e22642. https://doi.org/10.1002/ajp.22642

Whitehead, J.M., 1986. Development of feeding selectivity in mantled howling monkeys, Alouatta palliata, in: Else, J.G., Lee, P.C. (Eds.), Primate Ontogeny, Cognition and Social Behaviour. Cambridge University Press, Cambridge, pp. 105–117.

Whiten, A., 2005. The second inheritance system of chimpanzees and humans. Nature 437, 52–55. https://doi.org/10.1038/nature04023

Whiten, A., Custance, D.M., Gomez, J.-C., Teixidor, P., Bard, K.A., 1996. Imitative learning of artificial fruit processing in children (Homo sapiens) and chimpanzees (Pan troglodytes). Journal of comparative psychology 110, 3.

Whiten, A., Horner, V., de Waal, F.B.M., 2005. Conformity to cultural norms of tool use in chimpanzees. Nature 437, 737–740. https://doi.org/10.1038/nature04047

Whiten, A., Mesoudi, A., 2008. Establishing an experimental science of culture: animal social diffusion experiments. Philosophical Transactions of the Royal Society B: Biological Sciences 363, 3477–3488. https://doi.org/10.1098/rstb.2008.0134

Whiten, A., van de Waal, E., 2018. The pervasive role of social learning in primate lifetime development. Behavioral Ecology and Sociobiology 72. https://doi.org/10.1007/s00265-018-2489-3

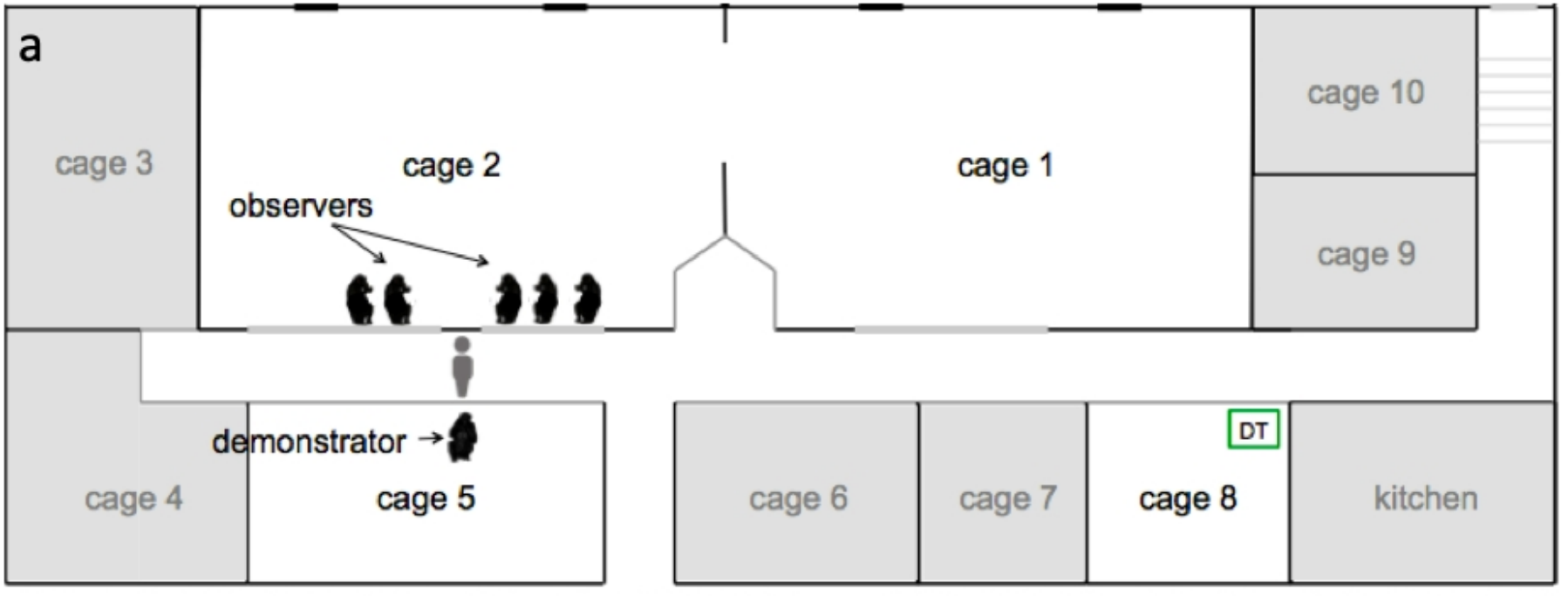
Whiten, A., van de Waal, E., 2016a. Social learning, culture and the 'socio-cultural brain' of human and non-human primates. Neuroscience & Biobehavioral Reviews. https://doi.org/10.1016/j.neubiorev.2016.12.018

Whiten, A., van de Waal, E., 2016b. Identifying and dissecting conformity in animals in the wild: further analysis of primate data. Animal Behaviour 122, e1–e4. https://doi.org/10.1016/j.anbehav.2016.09.010

Yamakoshi, G., 1998. Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: Possible implications for ecological importance of tool use. American Journal of Physical Anthropology 106, 283–295. https://doi.org/10.1002/(SICI)1096-8644(199807)106:3<283::AID-AJPA2>3.0.CO;2-O

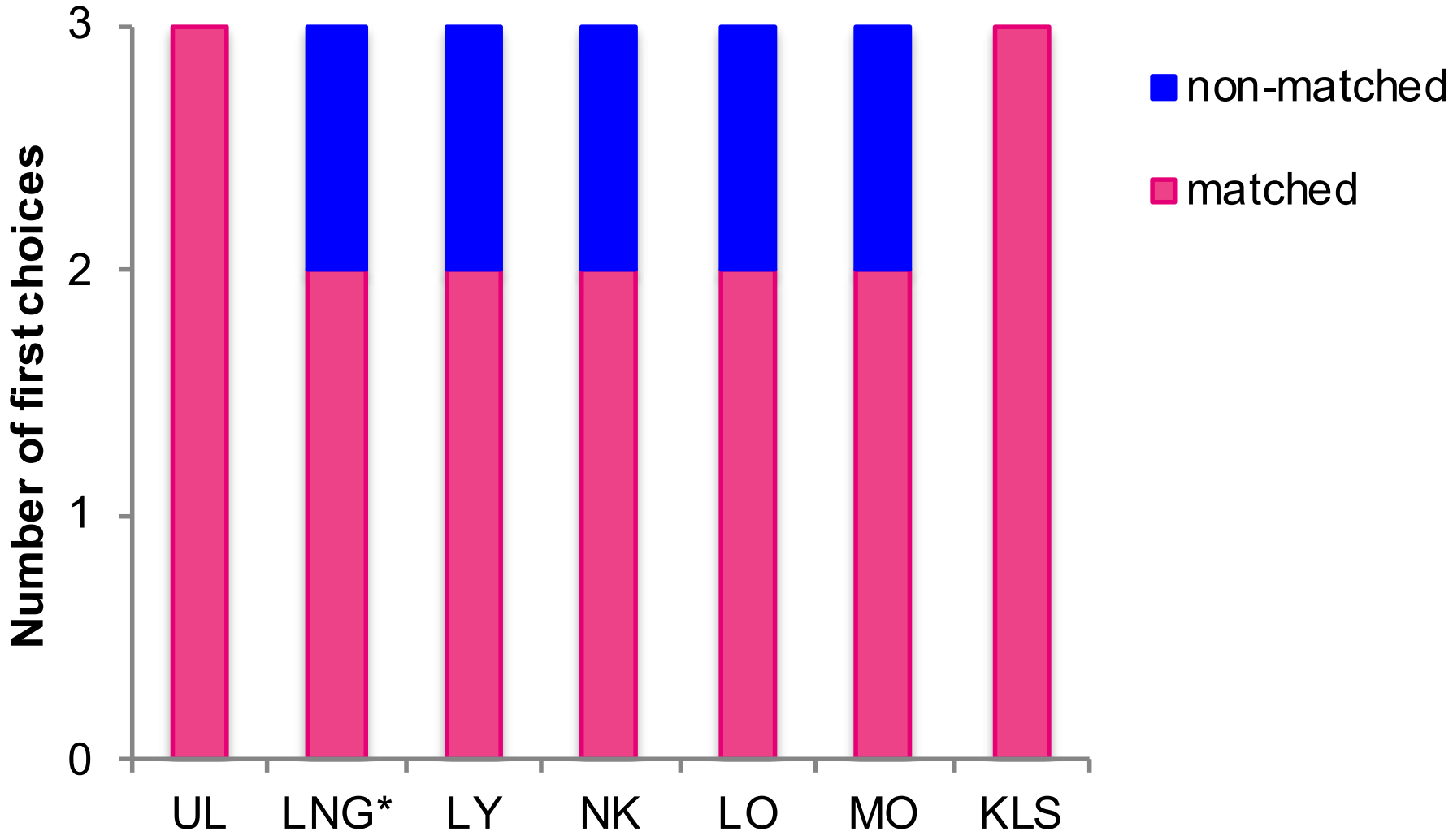
Zuberbühler, K., 2000. Interspecies semantic communication in two forest primates. Proceedings of the Royal Society of London. Series B: Biological Sciences 267, 713–718.

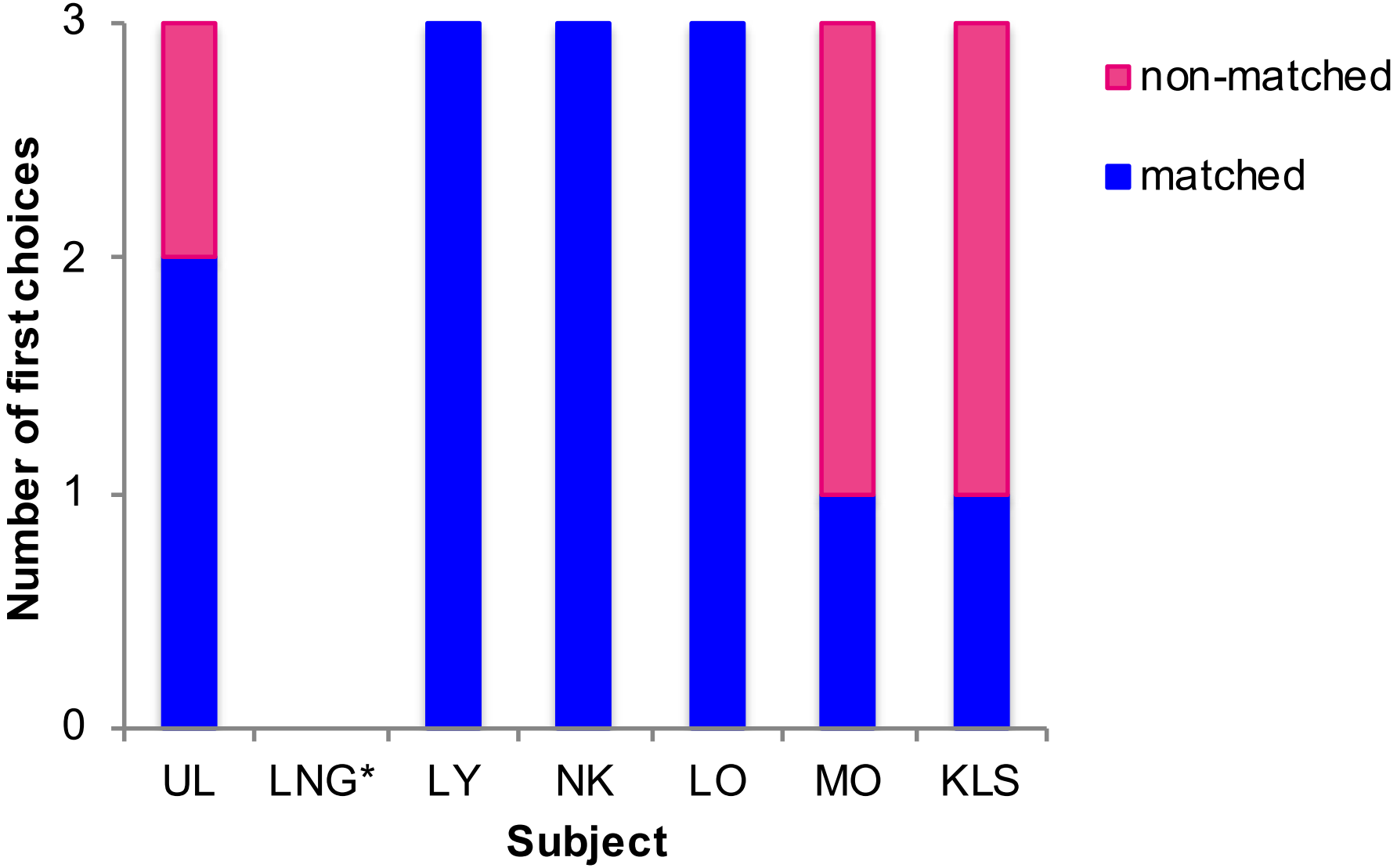
	I. Initial preference		II. New preference		III. Maintained preference			
KEL	P1  3 PD	OT x 5	B1  6 PD	OT x 5	B2  4 PD	OT x 5	B3  4 PD	OT x10
DW	P1  3 PD				P2  4 PD	OT x 5	P3  4 PD	OT x10

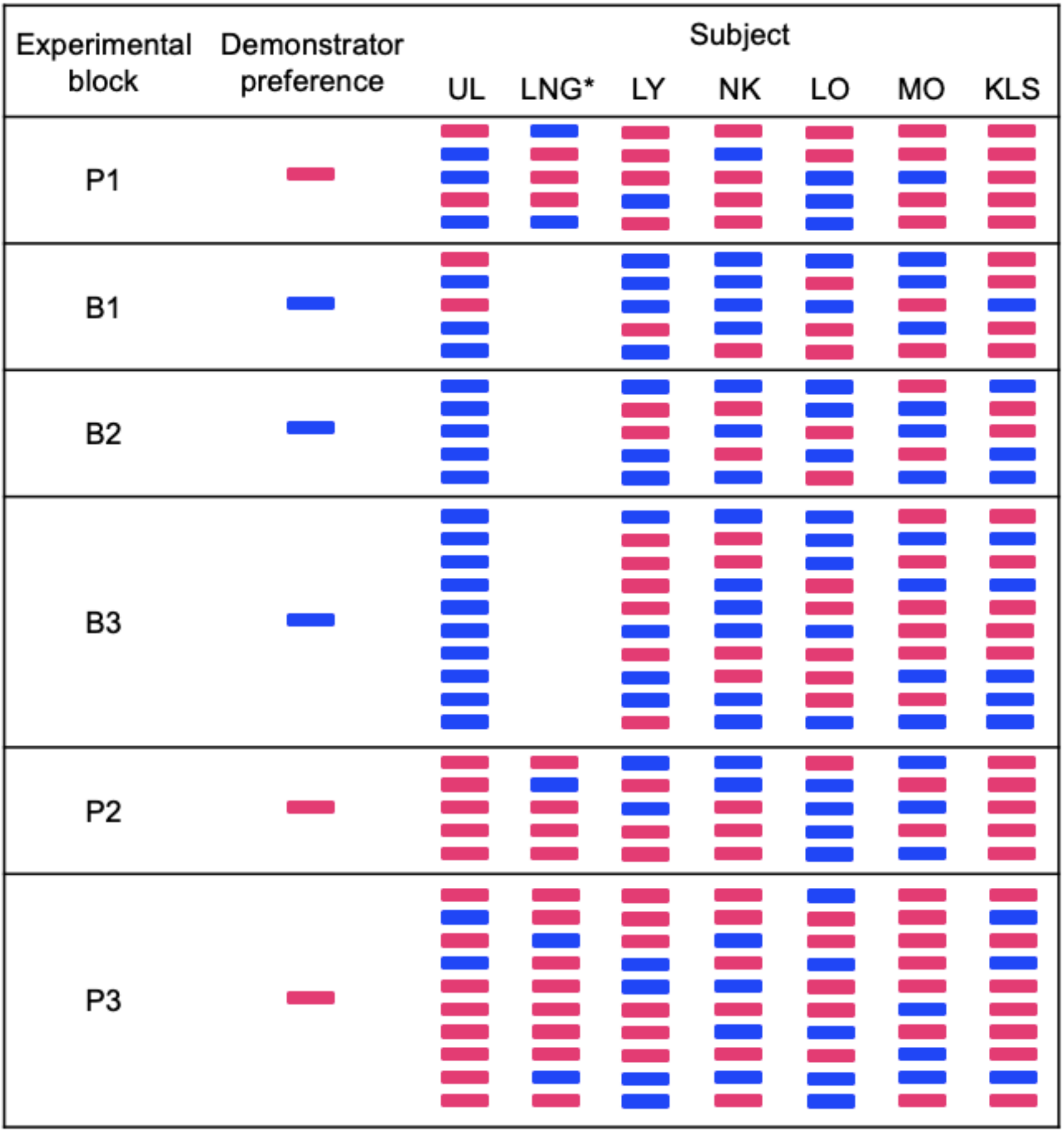

a
cage 3
cage 2
observers
cage 1
cage 10
cage 9
demonstrator
cage 4
cage 5
cage 6
cage 7
DT
cage 8
kitchen

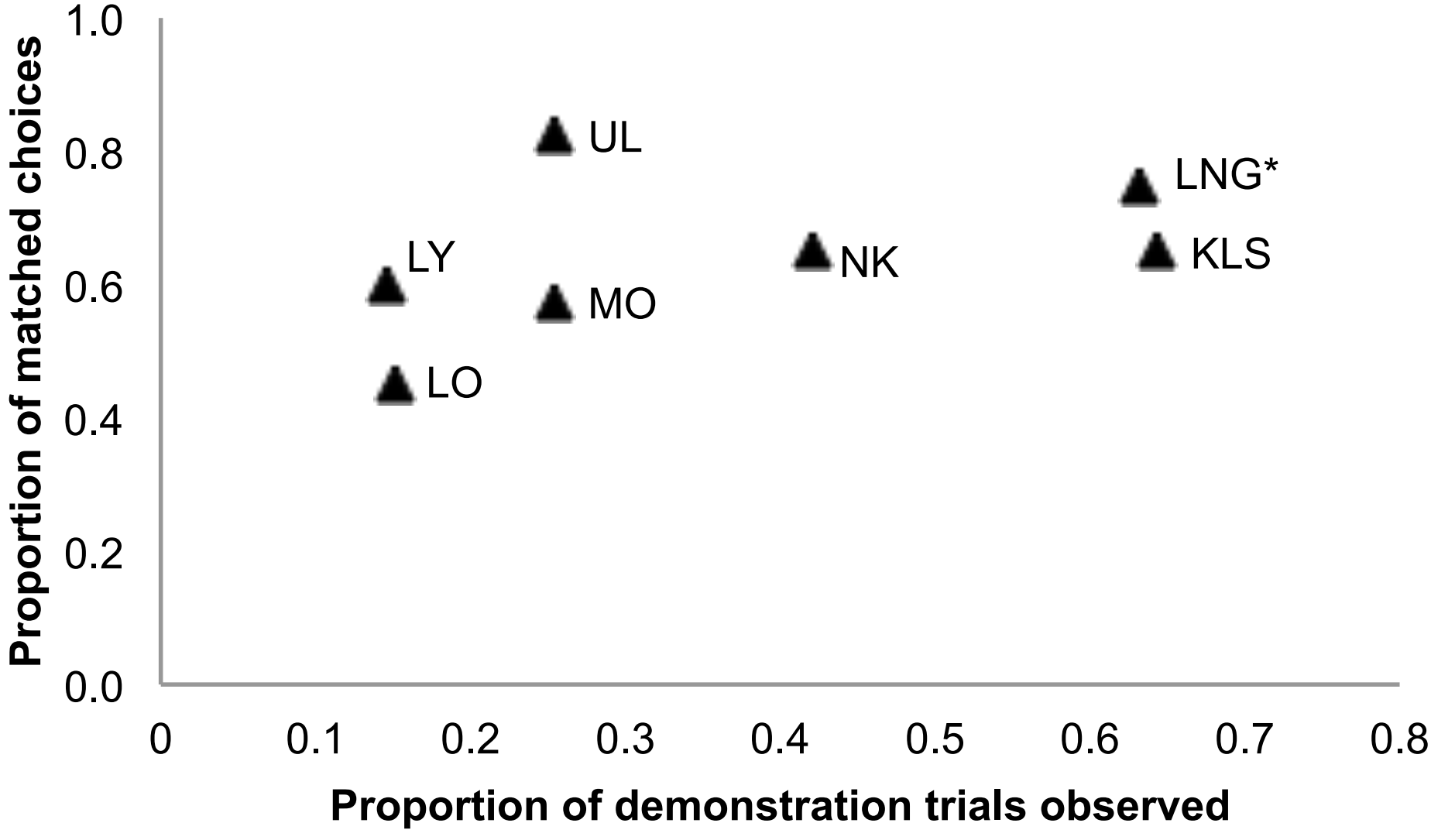

b


c


Number of first choices
3
2
1
0
UL
LNG*
LY
NK
LO
MO
KLS
non-matched
matched


3
2
1
0
Number of first choices
UL
LNG*
LY
NK
LO
MO
KLS
Subject
non-matched
matched


Experimental block
Demonstrator preference
Subject
UL
LNG*
LY
NK
LO
MO
KLS
P1
B1
B2
B3
P2
P3


Proportion of matched choices
1.0
0.8
0.6
0.4
0.2
0.0
UL
LNG*
LY
NK
KLS
MO
LO
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
Proportion of demonstration trials observed

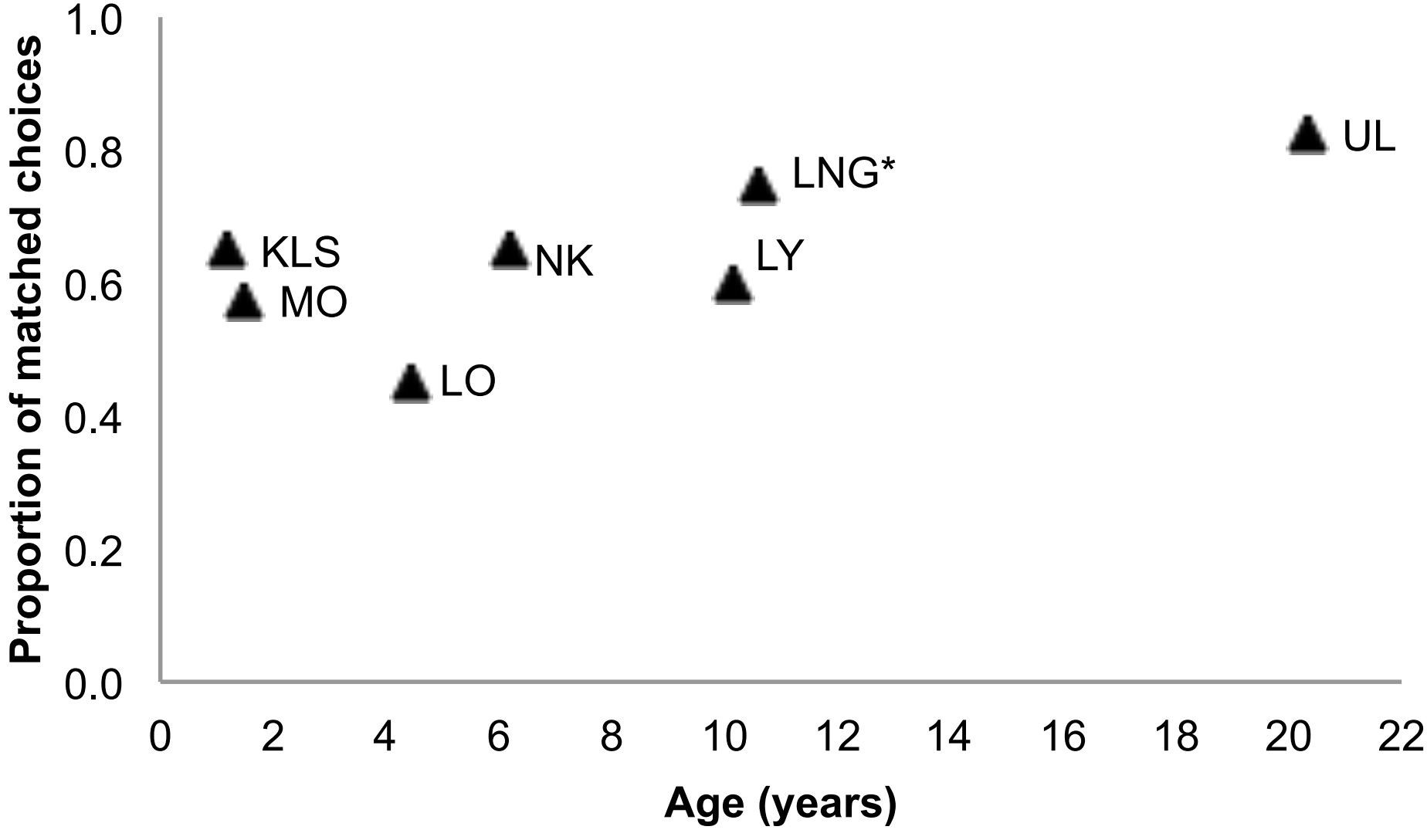

Proportion of matched choices
1.0
0.8
0.6
0.4
0.2
0.0
0
2
4
6
8
10
12
14
16
18
20
22
Age (years)
UL
LNG*
KLS
NK
LY
MO
LO

Table 1. Study subjects housed at La Vallée des Singes and role in the experiment

Individual	Sex	Birth year	Age-class	Role
Diwani (DW)	M	1996	Adult	Demonstrator
Kelele (KEL)*	M	2004	Adult	Demonstrator
Ulindi (UL)	F	1993	Adult	Observer
Lingala (LNG)	F	2003	Sub-adult	Observer
Lucy (LY)	F	2003	Sub-adult	Observer
Nakala (NK)*	F	2007	Juvenile	Observer
Loto (LO)	M	2009	Juvenile	Observer
Moko (MO)	M	2012	Infant	Observer
Khalessi (KLS)	F	2012	Infant	Observer

Individuals marked by an asterisk had the same father; age-class as defined by Kano (1984)

Table 2. Results of the logistic regression modelling the proportion of matched trials (N = 7).

	Estimate	Standard error	Z value	P	
Intercept	0.64	0.09	6.85	0.002	***
Age	7.33	1.60	4.59	0.010	*
Proportion of trials observed	1.65	0.50	3.32	0.029	*

Estimates are on a logit scale.

Table 3. Individual performance over all six experimental blocks

Subject	*N*	Proportion of demonstration trials observed	Food colour choice matched : unmatched	Performance (% matched)
UL	40	0.25	33:7	82.5
LNG	20	0.63	15:5	75.0
LY	40	0.14	24:16	60.0
NK	40	0.42	26:14	65.0
LO	40	0.15	18:22	45.0
MO	40	0.25	23:17	57.5
KLS	40	0.64	26:14	65.0

Proportion of demonstration trials observed, number of matched and unmatched choices and percentage of matched choices made by subjects. One individual (LNG) participated in the Observer Testing phase (OT) for only three of the six experimental blocks: P1, P2 & P3.